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Evolution

DNA systematics and evolution of the artiodactyl family Bovidae

(phylogeny/mtDNA sequences/rRNA genes/rapid cladogenesis)

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ABSTRACT **Nine additional sequences from representatives of different tribes of the family Bovidae were combined with six published artiodactyl sequences to provide orthologous mtDNA for investigation of bovid phylogeny and evolution. Each species was represented by a homologous 2.7-kilobase-pair stretch of mtDNA for the complete 12S and 16S rRNA genes and three adjacent tRNA genes. These data, when compared to other results, provided evidence for a monophyletic Bovidae and for two clades within the family: one including the tribes Boselaphini, Bovini, and Tragelaphini and another for an Antilopini/Neotragini grouping. All other intrafamilial relationships were only weakly supported. These sequence comparisons suggest that most bovid tribes originated early in the Miocene with all extant lineages present by ≈16–17 million years ago. Thus, bovid tribes provide an example of rapid cladogenesis, following the origin of families in the infraorder Pecora.**

The family Bovidae (infraorder Pecora, order Artiodactyla) includes 128 extant species in 45 recent genera, which are further grouped into 14 tribes, with most native to Africa (1). This family includes domesticated forms (goats, sheep, and cattle), the large herding antelopes of the African plains, and the small solitary, territorial forms usually found in more forested areas. The family represents the most diverse group of large mammals originating since the Miocene and has been studied extensively by those interested in paleoecology, biogeography, comparative anatomy, genetics, behavior, and physiology (2). Bovids are represented by a rich paleontological record; all extant tribes were present by 7 million years ago (MA). Yet despite the large amount of information known about them, their phylogenetic relationships remain uncertain.

The difficulty has not been in placing extant taxa into genera or tribes, but in determining the relationships among tribal groups (3). Many attempts have been made to resolve the phylogenetic relationships of bovid tribes (Fig. 1), although little, if any, consensus has been reached. This impasse is not simply a disagreement between molecules and morphology, because competing morphological (Fig. 1 *B*, *C*, and *E*) or molecular (Fig. 1 *A* and *D*) studies have disagreed among themselves. A convincing phylogenetic hypothesis is required to maximize the evolutionary importance of the facts available for bovids. In this study, we present additional molecular data in an attempt to provide better resolution of intertribal relationships within this family.

The characters for this study are obtained from nucleotide sequences for the mitochondrial rRNA gene complex, consisting of the complete gene sequences for the large 16S and small 12S subunits as well as their three flanking tRNAs ($tRNA^{Phe}$, $tRNA^{Val}$, and the 5′ end of $tRNA^{Leu}$). Each taxon was therefore represented by ≈2.7 kilobase pairs of contiguous coding mtDNA. In this study, nucleotide sequences* for nine additional representatives of bovid tribes were added to the published sequences for 2 other tribes and for four outgroup representatives of the infraorder Pecora (8, 9). The time of divergence for the bovid tribes [estimates ranging from 7 to 20 MA (7)] suggests that relationships within the family should be resolvable with this gene complex, which evolves at a rate suitable for this analysis (10). Of the 14 commonly recognized tribes of Bovidae, only 3 (Ovibovini, Peleini, and Rupicaprini) were not available for this sequencing study; their later inclusion will provide tests of the hypotheses developed herein.

MATERIALS AND METHODS

mtDNA sequences were collected from nine tribal representatives including *Aepyceros melampus* (AME), *Boselaphus tragocamelus* (BTR), *Cephalophus maxwelli* (CMA), *Damaliscus dorcas* (DDO), *Gazella thomsoni* (GTH), *Kobus ellipsiprymnus* (KEL), *Madoqua kirki* (MKI), *Oryx gazella* (OGA), and *Tragelaphus imberbis* (TIM). mtDNA isolation, cloning, and subsequent sequencing followed reported procedures (11). Additionally, large portions of the sequence for some species were collected by using PCR for amplification and sequencing of single-stranded DNA (12). Sequences were compared to those for other bovid and pecoran representatives [*Bos taurus* (BTA) and *Capra hircus* (CHI) versus *Antilocapra americana* (AAM), *Cervus unicolor* (CUN), *Giraffa camelopardalis* (GCA), and *Hydropotes inermis* (HIN), respectively] (8, 9). The nine additional sequences were aligned to each other and to the previously reported ones, as described before (9, 11). The four representatives from the other pecoran families (AAM, CUN, HIN, and GCA) were treated as outgroups and were included in the analyses to root the trees. These four outgroups span the taxonomic and mtDNA diversity present in the closest available relatives of the bovid study group (3, 9).

Several heuristic approaches implementing the parsimony procedure were conducted to find the most-parsimonious (MP) solution, including varying taxon addition, starting tree(s), and branch-swapping procedures. Analyses based on all mutations and transversions alone were conducted. Other approaches tested the stability of the MP results. Subsets of the entire 2.7-kilobase-pair stretch (i.e., treating the 12S and 16S rRNA genes alone and for transversions only) were analyzed separately to determine support among the various analyses. The more conservative changes (i.e., least saturated) of these subsets are the transversions, which convey the most reliable information about the oldest nodes of our MP phylogenies (10). Transversions were also used for date estimates because they have been documented to change linearly with time within the Artiodactyla (9).

Bootstrap resampling (based on 1000 resampling events) was also conducted to estimate the stability of the MP topologies (13). To determine how many extra steps were required to collapse each node, strict consensus trees were

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Abbreviations: MA, million years ago; MP, most-parsimonious; MYR, million years. The three-letter abbreviations for the species are given in *Materials and Methods*.

*The bovid sequences have been deposited in the GenBank data base (accession nos. M86493–M86501).

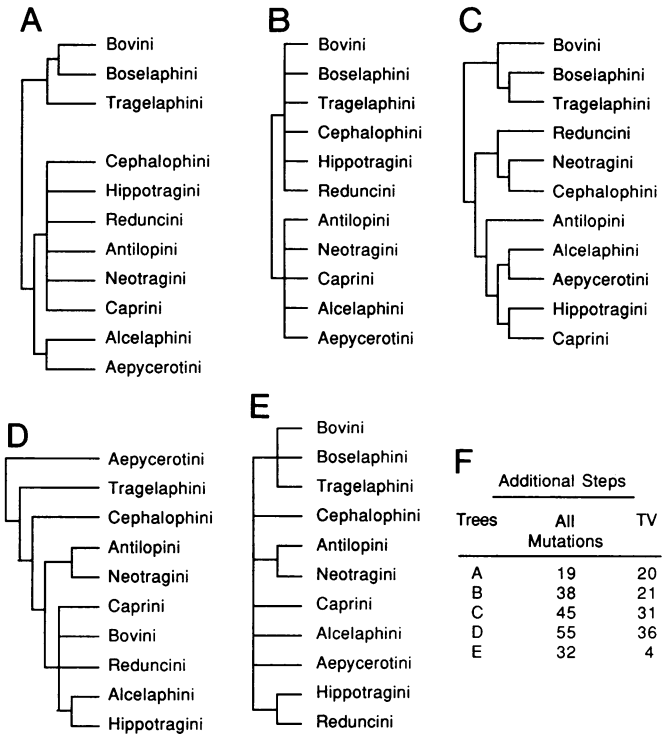

FIG. 1. Alternative hypotheses for relationships among the Bovidae based on a wide range of morphological and molecular characters. (*A–E*) Previously hypothesized trees. Only those with a majority of tribes represented are included here. (*F*) Listing of the number of additional steps necessary to optimize our sequence data onto each of these competing hypotheses by using either all mutations or transversions alone. The type of data that each phylogeny is based on and corresponding references are as follows: immunology (*A*; ref. 4), morphology of Aegodontia–Boodontia separation (*B*; see references in ref. 5), morphology and ecology (*C*; ref. 2), consensus tree based on allozymes and local branch swapping (*D*; ref. 6), morphological classification (*E*; ref. 7).

constructed for all arrangements, which were incrementally the same length or one step longer than before, noting which clades of the MP solutions collapsed at each point. By using these multiple approaches, the most stable groupings in the MP phylogenies were identified.

Branch lengths for the MP trees using all characters and transversions alone were estimated by using the probabilistic method of Fitch (14). Rate homogeneity was evaluated by the index of dispersion [$R(t)$ = (variance)/(mean of the branch lengths for sister lineages)] with values >2.5 taken as evidence of extensive rate heterogeneity (9, 15). For protein sequences used in clock calculations, $R(t)$ is usually <2–3. Mean percent pairwise divergences (±2 SE) for transversions alone were graphed for each tribe to the outgroup families to test further for rate heterogeneities. These comparisons to the outgroups make the assumption that the four pecoran families represented in this study are equally related to each other (i.e., the families reflect a star phylogeny or polychotomy), a hypothesis supported by earlier results (9).

The oldest fossils of the family Bovidae belong to the genus *Eotragus*, which has been assigned to the tribe Boselaphini (7). A rate of divergence for this tribe, using transversions only, was therefore calibrated according to these fossils and subsequently compared to that calculated from a different set of artiodactyl sequences (9). Times of divergence within the Bovidae were then estimated from these rates, after evaluating the extent of rate heterogeneity among the tribes (as described above).

RESULTS AND DISCUSSION

Pairwise Comparisons. Percent divergence was calculated for all pairwise comparisons of the 15 artiodactyl representatives. Within the Bovidae, the minimum divergence found (8.3%) was for the CMA to KEL comparison; the highest (12.1%) was from the comparisons of TIM to DDO and BTR to GTH (Table 1, upper diagonal). The most divergent value for interfamilial comparisons was 13.7% between AAM and DDO, whereas the least divergent pecoran comparison overlapped with the intrafamilial estimates for bovids (i.e., 11.1% for CMA to HIN). Within the Bovidae, maximum and minimum values of percent divergence, using transversions alone, varied from 2.2% (DDO to CMA) to 4.5% (TIM to GTH). Inter- and intrafamilial values once again broadly overlapped as percent transversions for bovids to the outgroups ranged from 2.9% (for CUN to CHI) to 4.6% (for AAM to DDO and BTR to HIN; Table 1, lower diagonal).

Minimally, transition/transversion (TS/TV) ratios were similar for both intra- and interfamilial comparisons (1.8 and 1.5, OGA to GTH versus GTH to HIN and BTR to HIN, respectively; complete pairwise results are not shown). TS/TV ratios were also maximally similar, with values of 3.3 within Bovidae (CHI to KEL) and 2.9 for pecorans (CHI to GCA). Thus, both estimates of divergence and TS/TV ratios for bovids versus Pecora as a whole were characterized by a considerable overlap in their respective ranges.

Table 1. Percent divergences for pairwise comparisons of bovid mtDNA sequences with divergences based on all mutations (above the diagonal) and those based on transversions alone (below the diagonal)

		AME	BTA	BTR	CHI	CMA	DDO	GTH	KEL	MKI	OGA	TIM	CUN	HIN	AAM	GCA
I.	AME	—	10.8	10.8	9.8	9.5	10.3	10.7	10.8	10.4	10.3	11.0	12.1	12.4	12.4	12.6
	BTA	2.6	—	10.3	11.1	10.4	11.4	11.0	11.7	11.2	11.2	10.4	12.2	12.8	13.1	13.0
	BTR	3.3	2.8	—	11.4	9.7	10.8	12.1	11.6	11.3	11.3	10.1	11.7	12.1	12.5	13.2
	CHI	2.4	2.8	3.7	—	9.3	9.8	10.1	10.7	10.3	9.6	11.8	11.2	11.6	11.6	12.6
	CMA	2.4	2.7	3.1	2.5	—	9.4	9.6	8.3	9.1	9.9	10.6	11.1	11.1	12.8	12.7
	DDO	3.1	3.1	3.8	2.8	2.2	—	12.0	11.2	10.8	10.1	12.1	12.5	12.3	13.7	13.6
	GTH	3.4	3.4	4.4	2.5	3.1	3.7	—	10.5	9.2	10.9	11.8	11.8	11.9	12.1	13.4
	KEL	2.8	2.9	3.5	2.4	2.3	3.3	3.0	—	10.5	11.3	11.9	11.3	11.7	12.9	12.9
	MKI	3.1	3.4	3.9	2.5	2.5	3.1	2.3	2.5	—	10.5	11.7	11.4	11.1	12.0	12.5
	OGA	2.9	3.3	4.0	2.5	2.8	3.0	3.7	2.9	3.3	—	11.8	12.2	12.6	13.0	13.4
	TIM	3.4	2.8	2.9	3.6	3.1	3.6	4.5	3.6	3.7	3.9	—	12.2	11.7	13.0	13.6
II.	CUN	3.4	3.4	3.9	2.9	3.4	3.7	3.7	3.2	3.3	4.2	3.7	—	7.3	11.8	12.5
	HIN	4.1	4.3	4.6	3.4	4.1	4.2	4.5	4.2	3.7	4.5	4.2	1.8	—	12.5	12.9
III.	AAM	4.0	3.8	4.4	3.1	4.1	4.6	3.9	3.6	3.6	4.2	4.0	3.5	4.2	—	13.2
IV.	GCA	4.0	3.8	4.4	3.0	4.1	4.3	4.1	3.6	3.9	4.4	4.4	3.6	4.3	3.6	—

Percent divergence for all mutations and transversions only (both uncorrected) were calculated as in ref. 9. Roman numerals refer to the study group (I, family Bovidae) and outgroups (II–IV, Cervidae, Antilocapridae, and Giraffidae, respectively).

Parsimony Patterns. A single fully resolved MP tree was obtained by parsimony analysis for all data (Fig. 2*A*). However, only four nodes for the study group were supported by over 80% of the bootstrap resampling trials including the monophyly of the Bovidae (88%), a clade consisting of Boselaphini/Bovini/Tragelaphini (88%), a Neotragini/Antilopini cluster (91%), and a Cephalophini/Reduncini group (84%). The other nodes for the family were less robust as they were supported by bootstrap scores of 24–58%. An alternative test of stability, the number of additional steps required to collapse the nodes of the best tree, gave similar results (Table 2). The same four clades supported by bootstrap analysis required 10 or more extra steps before collapsing (clades 3, 4, 6, and 10), whereas the others collapsed with the addition of six or fewer additional mutations.

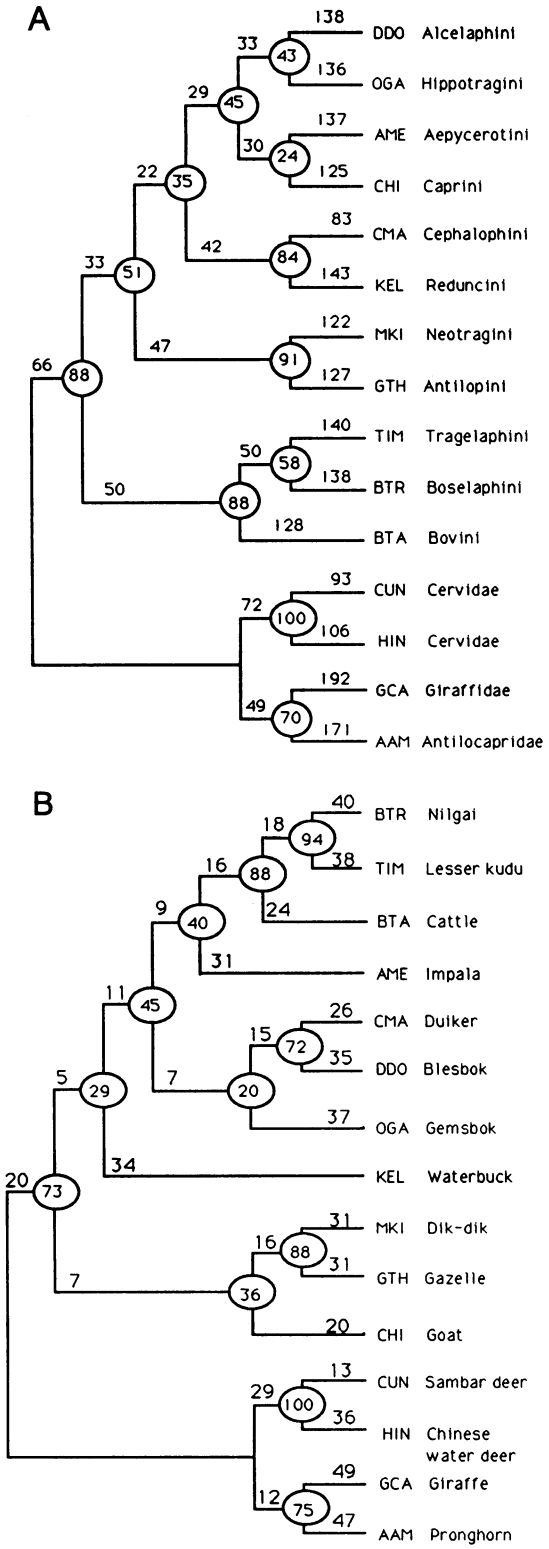

FIG. 2. MP trees for Bovidae. (*A*) By using all informative and variable data, the tree length is 2121 mutations, and the retention index (16) is 0.31. (*B*) By using only transversions, the tree length is 477 mutations, and the retention index is 0.43. For both *A* and *B*, values at the circled nodes represent bootstrap replication scores, whereas those above the internodes refer to branch lengths (13, 14). For both trees, change among bovids is largely limited to terminal branches, with relatively little along their internal branches (ratio of terminal branch lengths to total length is 84% and 81%, respectively). The root for each solution has been arbitrarily drawn between the study group and outgroups. To assign a root for the infraorder Pecora requires the inclusion of more distant outgroups (e.g., *Tragulus* of the infraorder Tragulina), which, in turn, results in a further test of bovid monophyly (9). In *A*, the three-letter abbreviations for the species are presented with their tribes (study group) or families (outgroup), whereas in *B*, they are included with their common names.

Except for the Cephalophini/Reduncini clade, the same best-supported groupings as above were corroborated by parsimony analysis using more conservative changes, the transversions. A single MP tree was found (Fig. 2*B*); the monophyly of Bovidae, the Antilopini/Neotragini clade, and the Boselaphini/Bovini/Tragelaphini cluster was supported by bootstrap scores >72% and four or more extra mutations (Table 2). Furthermore, a Boselaphini/Tragelaphini cluster was supported by 94% of the bootstrap replicates and 10 additional mutations, both of which were the highest values for bovids in the transversion parsimony tree. Instead of a Cephalophini/Reduncini clade, Cephalophini now grouped with Alcelaphini at a bootstrap score of 72% and by six extra steps (Fig. 2 and Table 2). All other clades of the MP tree for transversions were defined by bootstrap scores of <50% and fewer than four extra steps.

Separate analyses for the large and small subunits of mitochondrial rRNA led to incongruent results. The MP tree for the 12S rRNA gene sequences supported the same robust nodes as did the complete matrix (see above), except that the Cephalophini/Reduncini clade was not replicated. The MKI/GTH clade and the monophyly of Bovidae were rejected by the 16S rRNA gene, although the CMA/KEL clade was repeated here along with the Boselaphini/Bovini/Tragelaphini cluster. These separate analyses were based on all mutations. When transversions alone were used, the same results with regard to bovid monophyly, an Antilopini/Neotragini clade, and a Boselaphini/Bovini/Tragelaphini cluster were obtained for the separate genes. However, in all cases, the placement of other tribes varied considerably.

Previous phylogenetic hypotheses of bovid relationships required an additional 19–55 extra steps for all mutations and 4–36 extra steps for transversions alone, relative to their respective MP solutions (Figs. 1 and 2). These differences in tree length were conservative estimates, since four of the five arrangements included major polychotomies, which were resolved as parsimonious dichotomies by the optimization procedure. Thus, these estimates represent minimum differences in the tree score. The phylogeny of Lowenstein (4) (Fig. 1*A*) has the lowest length compared to the other four, when all mutations were counted. For transversions only, the arrangement of Gentry (7) required 5 times fewer mutations than the next best topology (that of Lowenstein; cf. Fig. 1 *A* and *E*).

Evolutionary Rates. Calculations of $R(t)$ for all characters revealed only two instances of extensive rate differences according to our criterion of 2.5 (Table 2). These involved slower rates for BTA and CMA. When only transversions

Table 2. Indices of dispersion [$R(t)$] and the number of additional steps needed to collapse each clade of the MP trees for all characters and transversions alone (Fig. 2 *A* and *B*, respectively)

All character analysis			Transversion analysis		
Clade	Extra steps	$R(t)$	Clade	Extra steps	$R(t)$
1 DDO/OGA	4	0.0	1 OGA/3	1	0.4
2 AME/CHI	3	0.3	2 AME/6	3	5.2
3 CMA/KEL	10	8.0	3 CMA/DDO	6	0.7
4 MKI/GTH	20	0.1	4 MKI/GTH	7	0.0
5 TIM/BTR	5	0.0	5 TIM/BTR	10	0.0
6 BTA/5	10	5.9	6 BTA/5	8	6.7
7 1/2	6	0.1	7 1/2	3	0.8
8 3/7	4	2.2	8 KEL/7	1	5.8
9 4/8	5	2.1	9 CHI/4	1	5.4
10 6/9	11	0.3	10 8/9	4	0.0
11 CUN/HIN	35	0.4	11 CUN/HIN	20	5.4
12 AAM/GCA	3	0.6	12 AAM/GCA	3	0.0
13 11/12	11	4.3	13 11/12	4	0.2

For each analysis, clades are assigned numbers for later identification in the group listings (e.g., clade 3 for the transversion results corresponds to CMA and DDO).

were counted, four such instances were revealed, involving AME, BTA, CHI, and KEL.

Some rate differences were detected by the relative rate tests of the bovid tribes to the outgroup families, using transversions alone (Fig. 3*A*). The transversion rate of sequence evolution for CHI was significantly less than that for all other bovids. AME, BTA, CMA, and KEL were also at the lower end of the range, in agreement with their estimates of $R(t)$. However, although these rate heterogeneities existed, they were regarded as minor, because of their small relative differences. For CHI and BTR (the lowest and highest values, respectively), transversion rates differed by only 30% (3.1% versus 4.4%).

Bovid Phylogeny. A parsimony analysis of all characters results in few additional nodes with substantially greater support than that provided by transversions alone (Table 2 and Fig. 2). This result suggests that the phylogenetically informative characters on which the tree for all mutations is based are mainly transversions. Thus, little is gained from the transitions and gaps at these levels, and indeed, their inclusion could be expected to obscure the actual relationships (10). The unusual phylogenetic results from the analysis of all characters for the 16S rRNA gene can be attributed to this problem. When transversions were analyzed alone, the results for the 16S rRNA gene were more consistent with the other analyses (see above), which supports the contention that the more rapidly evolving transitions were contributing noise to phylogenetic inference.

The bootstrap scores for the placement of CMA highlight the need to evaluate the robustness of groupings by multiple means, rather than by any single approach. In the MP tree for all mutations, CMA clusters with KEL instead of DDO as when only transversions are counted (Fig. 2). These different arrangements are supported by bootstrap scores of 84% and 72%, respectively. That the more conservative transversions place CMA in a position conflicting with one supported by a higher bootstrap score emphasizes the need to use different approaches to evaluate the robustness and reliability of individual clades.

By using multiple tests to evaluate robustness, only three intertribal groupings of Bovidae are consequently recognized as strongly supported: (*i*) the monophyly of the family itself; (*ii*) the clustering of Boselaphinae, Bovinae, and Tragelaphinae; and (*iii*) the grouping of Antilopinae and Neotragini.

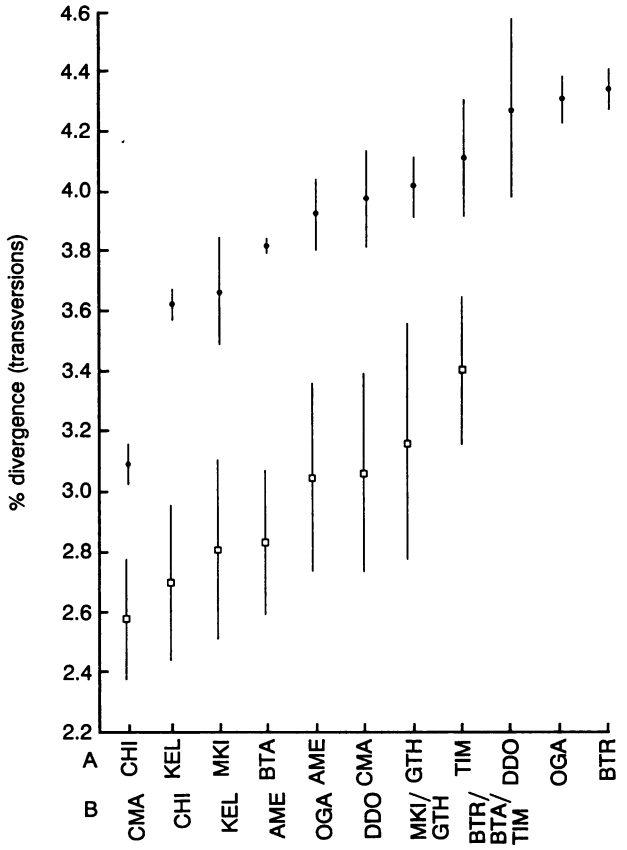

FIG. 3. Mean percent divergence (±2 SE), using transversions. (*A*) Mean divergences of each tribal representative to the three pecoran outgroup families (with CUN and HIN averaged for Cervidae) (●). (*B*) Comparisons of each major lineage to all others within the Bovidae (□). Here, the intertribal clades (MKI/GTH and BTA/BTR/TIM) are treated as single lineages (following our phylogenetic conclusions; see text) and are therefore averaged when compared to the other tribes.

Each of these groups shares relatively high bootstrap scores (88–91% and 73–88% for all mutations and transversions, respectively), large numbers of extra mutations (10–20 and 4–8 additional steps), and stability across different subsets and treatments of the data (e.g., transversions alone for 12S rRNA versus 16S rRNA gene sequences) (Fig. 2, Table 2, and see above). The recognition of these three groups is also based on their congruence with the phylogenetic results of other data (Fig. 1). The Antilopini/Neotragini clade is corroborated by the allozyme and one morphological phylogeny (Fig. 1 *D* and *E*), whereas the Boselaphini/Bovini/Tragelaphini cluster is concordant with the immunological, morphological, and ecological trees (Fig. 1 *A*, *C*, and *E*). For the latter group, only the allozyme tree is incongruent (Fig. 1*D*), whereas for the Antilopini/Neotragini clade, only the morphological/ecological phylogeny (Fig. 1*C*) disagrees. With regard to bovid monophyly, this hypothesis has been questioned (9). However, the current mtDNA results in its favor are corroborated by the unique and unambiguous morphological synapomorphies, bony horn cores with keratinous sheaths and very large foramina ovales (17). Thus, the recognition of these clades as robust is supported by independent evidence in addition to the mtDNA sequences.

Rapid Cladogenesis. In contrast to the three groups supported above, the relationships of other bovid tribes remain poorly understood and must be considered unresolved. Thus, like previous investigations (as reflected by the extensive polychotomies in their trees; Fig. 1), the mtDNA sequences have largely failed to resolve the intertribal relationships of

bovids. A similar situation was obtained for the families of Pecora by a previous study of mtDNA sequences (9). This investigation concluded that the pecoran families were the result of a rapid radiation, occurring over a brief 5 million years (MYR), 23–28 MA in the Late Oligocene to Early Miocene. Such rapid cladogenesis offered little time for mutations to accumulate along common stems, thereby making recovery of the phylogeny difficult and disagreement among investigators likely. Our mtDNA results support a similar hypothesis of rapid cladogenesis in the family Bovidae, thereby providing a comparable explanation as to why resolution of bovid relationships has also been problematic.

One important line of evidence in favor of this hypothesis comes from a consideration of the Antilopini/Neotragini clade, one of our three robust groupings. The fossil record for Antilopini dates back to at least 16–17 MA (3), suggesting that the tribe Neotragini is at least this old too. Furthermore, these two differ by 2.3% transversions, which represents the second smallest intertribal value (2.2% for CMA to DDO is the least; Table 1). Taken together, these observations suggest that the eight major lineages of bovids (the BTA/BTR/TIM and GTH/MKI clades plus the other six tribes separately) are older than 16–17 MA. Given that the pecoran families radiated 23–28 MA (9), these results support the hypothesis that the major lineages of bovids originated sometime between 16 and 17 MA in the Early Miocene (the Antilopini/Neotragini split) and 23–28 MA in the Late Oligocene to Early Miocene (the radiation of Pecora).

Although rate heterogeneities exist, the relative rate tests suggest that these differences are small enough to permit clock calculations with the mtDNA sequences by using the conservative transversions (Fig. 3*A*). BTA, TIM, and BTR form one of our three robust clades; the latter differs from the former two by an average of 2.8% transversions (Table 1). Given a divergence time of 20–21 MA for Boselaphini (3), the evolutionary rate of transversions for BTR is calibrated at 0.14% transversions per MA. This estimate, based on the oldest fossil evidence for Bovidae, agrees with that reported for a different set of artiodactyl sequences (ref. 9; see their figure 5) as well as that for the Antilopini/Neotragini split (2.3% transversions per 16–17 MA = 0.14% transversions per MA; see above). Such agreement within the family and with Pecora, when coupled with the relative rate tests (Fig. 3*A*), supports the conclusion that rates of evolution are at least similar and are therefore appropriate for estimating divergence times within the family.

The BTA/BTR/TIM clade exhibits the greatest average divergence among the eight major lineages of the family (3.4% transversions; Fig. 3*B*). By using an average rate of 0.14% transversions per MA, a clock calculation places the start of the bovid radiation at 24 MA in the Early Miocene. A lower bound of 16–17 MA for this radiation is supported by the fossil evidence for Antilopini/Neotragini (see above), thereby limiting the origin of the major bovid lineages to 7–8 MYR in the Early Miocene. Thus, according to these dates, the rapid origin of pecoran families about 23–28 MA (9) was followed by a second radiation in the family Bovidae approximately 16 or 17–24 MA. These successive radiations resulted in the four major families of Pecora (Antilocapridae, Bovidae, Cervidae, and Giraffidae) as well as in the eight main lines of bovids recognized here.

Hypothesis Testing. The major conclusion of this study is that two successive series of rapid cladogenesis occurred within the infraorder Pecora during the Late Oligocene to Early Miocene (approximately 23–28 MA to 16 or 17–24 MA). An initial radiation of pecoran families, lasting 5 MYR, was followed by one of 7–8 MYR for the bovids. Our dates for the bovid radiation correlate with the emergence of savanna between 18 and 23 MA in Africa (the major center of diversification for the family) (18). According to this interpretation, the radiation of bovids is related to the first appearances of savanna in woodland savanna habitat. Further development of savanna to an open habitat thereby led to the specializations for grazing associated with many tribes in this family. As the major lineages of bovids predate open savanna according to this hypothesis, morphological specializations for this habitat must have been acquired independently, which may explain why the aegodont/boodont patterns of cranial morphology and dentition have been regarded as such poor indicators of phylogenetic relationship (6).

The origin of major bovid lineages is therefore tied to Early Miocene events, rather than to more recent ones (6, 19). However, as many bovid tribes date back in the fossil record only about 6–7 MA (3), the question is raised as to why representatives from more lineages are not known from the Early Miocene. A major prediction of this hypothesis therefore is that many Early Miocene bovids are yet to be found (i.e., the current fossil record of the family is largely incomplete). Alternatively, some representatives may already exist in collections, but remain unclassified to tribe due to problems in identifying their diagnostic features. Thus, we argue that additional fossil material and analyses are now needed to understand better the early origins and history of the family Bovidae (3) and that, when coupled with comparable sequence data for Ovibovini, Peleini, and Rupicaprini, will provide critical tests of our hypotheses.

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